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Evaluation of native warm-season grass cultivars for riparian zones

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Abstract: Aerenchyma are air-filled spaces in the root cortex that help maintain oxygen supply to roots in saturated soils. We examined aerenchyma formation in roots and its effect on the suitability of 26 native warm-season grass cultivars from six species for use in riparian areas. In a greenhouse study, all cultivars exhibited extensive aerenchyma formation in well-drained soil, and percent aerenchyma was greater in the well-drained control than in the saturated treatment (89% versus 71%, respectively). However, the presence of extensive aerenchyma development did not guarantee good root growth under anaerobic conditions. Suitable plant materials for inclusion in riparian areas were found among four of the six warm-season species examined, although a wide range in suitability was observed within species where multiple cultivars were tested. Nine cultivars representing a range of responses were further evaluated at four field locations subjected to flooding and soil saturation. Red River prairie cordgrass (*Spartina pectinata* L.) provided superior performance at all locations. The worst performing cultivars in the greenhouse study also performed poorly in the field. However, not all cultivars that performed well in the greenhouse also performed well in the field. Osage Indiangrass (*Sorghastrum nutans* L.) was the third ranked cultivar for flooding tolerance in the greenhouse but had acceptable performance at only one of the four field sites. Conversely, Meadowcrest eastern gamagrass (*Tripsacum dactyloides* L.) exhibited only moderate flooding tolerance in the pot study but had among the lowest mortality, highest vigor, and highest biomass at three of the four locations. Controlled environment studies were useful for eliminating unacceptable cultivars, but field studies were necessary to identify suitable material for riparian areas.

Key words: aerenchyma—flooding tolerance—riparian buffers—warm-season grasses

Plants growing in riparian buffers are subjected to a variety of stresses, including reduced nutrient uptake and reduced oxygen availability due to periodic flooding of their habitat (Visser et al. 2000a). In response to waterlogged conditions, many plant species develop aerenchyma in their roots. These large intercellular spaces allow movement of oxygen from shoots into submerged root tissues, thus allowing continued growth and nutrient uptake. Aerenchyma may either form constitutively during the ontogeny of a root through the separation of cortical cells, or facultatively in response to flooding or other environmental triggers by breaking down or tearing of existing cell walls (Esau 1965). Aerenchyma have been previously observed in several North American native warm-season grass species, including eastern gamagrass (*Tripsacum dactyloides* [Clark et al. 1998; Ray et al. 1998]), *Andropogon* species (*Andropogon gayanus* [Baruch and Merida 1995]), *Spartina* species (*Spartina patens* [Pezeshke et al. 1993], *Spartina alterniflora* [Naidoo et al. 1992]), and *Panicum virgatum* (R.W. Zobel unpublished data). Various studies have suggested that a positive relationship exists between the frequency of flooding experienced by a given species and the ability of that species to form aerenchyma (Visser et al. 2000a; Vasellati et al. 2001). Similarly, increased aerenchyma formation has been positively related to flooding tolerance (Vasellati et al. 2001). However, anatomical features that facilitate growth in waterlogged soils may cause limitations for root function under well-drained conditions by negatively influencing the rate of water and solute uptake by roots (McDonald et al. 2002).

Native warm-season grasses are a potentially important component of riparian buffers designed to reduce nonpoint-source pollution (nutrients, pesticides, and pathogens) of eastern US streams and rivers (Lee et al. 1999; Blanco-Canqui et al. 2004; Lin et al. 2004). USDA Natural Resources Conservation Service (NRCS) personnel are often called on to provide guidance as to what plant materials are suitable for various conservation applications. However, little is known about the performance of NRCS warm-season grass cultivars under saturated soil conditions. The objectives of this study were to (1) under controlled conditions, quantify differences in root production and aerenchyma formation among warm-season grass cultivars in anaerobic saturated soil conditions, such as those that would be commonly found along bottomlands adjacent to streams and other water sources; and (2) test differences observed in greenhouse studies under field conditions to determine if information obtained under controlled conditions can adequately identify suitable materials for riparian buffers. This information could serve to improve field office recommendations to landowners for selecting the best-suited material for saturated sites.

Material and Methods

Cultivar Screening. Initial cultivar screening included 26 warm-season grass cultivars from six species native to North America. The following species and cultivars were included: (1) big bluestem (*Andropogon gerardii* Vitman) cv. Kaw, Roundtree, OH-370, Suther, Niagara, Bison, Earl and Bonilla; (2) little bluestem (*Schizachyrium scoparium* Michx.) cv. Suther; (3) switchgrass (*Panicum virgatum* L.) cv. Blackwell, Kanlow, Shelter, Hightide, Contract, Forestburg, Alamo, Cave-in-Rock and Dacotah; (4) Indiangrass (*Sorghastrum nutans* L.) cv. Cheyenne, Tomahawk, Osage,

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Suther and Rumsey; (5) prairie cordgrass (*Spartina pectinata* L.) cv. Red River; and (6) eastern gamagrass (*Tripsacum dactyloides* L.) cv. Meadowcrest and Pete. The study was conducted in a greenhouse at the NRCS Cape May Plant Materials Center, Cape May, New Jersey.

Breeder quality seed of each cultivar were germinated in Petri dishes and then was transplanted into 10 × 10 × 35 cm (4 × 4 × 14 in) pots filled with sandy topsoil (90% sand) purchased from a sand and gravel company near the Cape May location. Gravimetric field capacity of the soil was 0.13 g g^{-1} (13%), and when fully saturated, soil moisture content was 0.17 g g^{-1}. Seedlings were placed in a greenhouse providing a 14-hour photoperiod and day and night temperatures of 27°C to 29°C and 16°C to 18°C, (81°F to 84°F and 61°F to 64°F) in the early spring of 2000. In May 2000, pots were relocated to an outdoor holding area and were allowed to grow for one season. The sides of the holding area were sunk into the ground about 60 cm (24 in) and were lined with cinderblocks, but the top was open to the atmosphere. Pots received natural precipitation and were hand-watered, as necessary.

In early February 2001, dormant plants were removed from their pots, and roots and shoots were trimmed to 15 cm (6 in). Trimmed plants were then transplanted to 15 × 120 cm (6 × 48 in) polyvinyl chloride (PVC) pots with wire-mesh bottoms. Pots were filled with the same soil as previously used. Plants were again placed in a heated greenhouse with 12 replicates per cultivar. Six replicates were watered to maintain adequate soil moisture content but were allowed to drain freely (control treatment), while six replicates were placed in standing water to a depth of 60 cm and were also watered from above to maintain adequate surface soil water availability (saturated treatment). A few selected plants were harvested periodically during April and May 2001 to determine when roots from most of the cultivars had reached the bottom of the pots in the control treatment.

On May 22, 2001, plants were harvested by laying each pot on its side and making longitudinal cuts so that one-half of the PVC pot could be removed, exposing the length of the soil core. Two-centimeter thick soil sections were then removed from the top, middle (just below the water line), and bottom of each pot for root-length density analysis. Roots were washed free of soil by placing roots on a fine-mesh screen and gently running water over the screen to separate roots from soil. Washed roots were spread out on a thin film of water in a glass tray and were scanned for root length determination using an Epson Perfection 4870 scanner. A flood tolerance ratio was estimated for each cultivar by dividing root length in the middle section of the saturated treatment by root length in the middle section of the control. A flood tolerance ratio >1 indicated that root growth in the saturated treatment was greater than in the control, whereas a ratio <1 indicated that root growth was inhibited by the saturated conditions. Two to three, 3 cm (1.2 in) long root segments were also collected just below the sections used for root-length measurements and were placed in FAA (formalin–acetic acid–alcohol [ethanol]) for aerenchyma determination. Approximately 100 to 200 g (0.22 to 0.44 lb) of soil were also collected from each area for soil moisture calculations. Moisture content was determined by drying at 105°C (221°F) for 72 hours then weighing the dried samples. No aboveground data were collected.

Root sections were prepared for sectioning according to procedures described in Volenec and Nelson (1981). Briefly, roots were dehydrated in a series of solutions containing differing proportions of ethanol and t-butanol and then were embedded in paraffin. Tissues were sectioned transversely with a microtome, were mounted on microscope slides, and were stained with safranin O. Aerenchyma content for roots collected from the middle section of each pot was visually estimated as the percentage of the cortex that was occupied by air spaces. Evaluations were conducted independently by two individuals.

All pots in the saturated treatment were placed within a single specially constructed wood frame lined with heavy-duty plastic, which could be filled with water to the desired level. Pots in the control treatment were also grouped together in a single group. Replicates within each water treatment were arranged in a randomized-block design. Because of time limitations, four of the six replications in each moisture treatment were harvested. Aerenchyma determinations were only made for roots from the middle section. Data were analyzed as a split-plot design using SAS Proc GLM (SAS 2002), with moisture treatments as main plots and cultivars as subplots. Because moisture treatments could not be randomized, no statistical comparison was made between the control and saturated treatments. Percentage aerenchyma was square root transformed prior to statistical analysis. The flood tolerance ratio was calculated for paired pots from each replication and then data were square-root transformed. Differences among means were determined to be significant at $p < 0.05$. All transformed data were back-transformed for presentation.

Field Study. Nine cultivars from the initial screening were selected for further evaluation in the field. The cultivars selected included Bonilla, Niagara, and Suther big bluestem (BB), Osage and Suther Indiangrass (IG), Shelter and Hightide switchgrass (SG), Meadowcrest eastern gamagrass (EG), and Red River prairie cordgrass (PC). These cultivars represented the entire range of root growth responses and, with the exceptions of Bonilla BB (South Dakota), Osage IG (Kansas), and Red River PC (North Dakota), were selected from cultivars originating in the northeastern United States. Seeds were sown into 164 mL cone-tainers (Stuewe & Sons, Corvalis, Oregon), were filled with potting soil, and were placed in the greenhouse in November 2003. Seedlings were watered as needed and were fertilized monthly with liquid Peter's Professional All Purpose Plant Food 20/20/20 fertilizer. Greenhouse day and night temperatures were set at 25°C and 18°C (77°F and 64°F). Day length was extended to 14 hours with metal halide lamps suspended from the ceiling.

Seedlings were transplanted at the research locations on the following dates: Wye Research Center, April 19 to 20, 2004; Mattern watershed, May 10, 2004; Big Flats Plant Materials Center, May 11, 2004; and Lamb's Creek Recreation Area, May 13, 2004. Each cultivar was planted in three rows, with 17 plants per row. Plant spacing was 30 cm (12 in) between and within rows. Treatments were replicated four times in a randomized complete block design. Data for each cultivar were only collected from the middle row with the two outside rows as borders. The plants on each end of the middle row also served as borders, giving 15 plants per experimental unit. Two subsurface saturation sensors (Srinivasan et al. 2000) were installed at each site, except for Lamb's Creek where deep flood waters prevented their use. One sensor was placed near the stream bank or other water course

Table 1
Site description for field sites used to test flooding tolerance of warm-season grass cultivars.

Site	Coordinates	Elevation (m)	Annual rainfall (mm)	Annual T_{air} (°C)	Soil type	Brief site description
Big Flats, New York	42.1°N 77.0°W	274	892	8.5	Silt loam	Sloping stream bank
Lamb's Creek, Pennsylvania	41.5°N 77.1°W	331	850	7.8	Silt-loam	Reservoir flood plain
Mattern Watershed, Pennsylvania	40.7°N 76.6°W	270	1,060	9.3	Clay, silty-clay	Watershed head waters
Wye Research Center, Maryland	38.5°N 76.1°W	0	1,100	13.2	Sandy loam, loam	Coastal wetland

Note: T_{air} = air temperature.

and the other was placed near the top of the plot.

Field studies were conducted in four locations in New York, Pennsylvania, and Maryland. Environmental and physical characteristics for each site are summarized in table 1. The northernmost location was along the banks of Winfield Creek, located on the USDA NRCS, Big Flats Plant Materials Center near Corning, New York. The stream bank at the site was located on an Orrville silt loam soil (Fine-loamy, mixed, active, nonacid, mesic Fluventic Endoaquept) that had been shaped with a bulldozer about 25 years prior to the experiment to provide a gentle slope, with a drop in elevation of about 1.2 m (4 ft) from the top of the bank to the streambed. Plots were oriented perpendicular to the stream. Plants near the bottom of the plots were about 0.6 m (2 ft) above the streambed. The stream is subject to periodic flooding after storms and during spring melt, but it can also be dry following periods of little or no rain during the summer. Soil profiles showed the presence of redoximorphic features throughout, indicating that the site had a seasonally high water table that appeared to come very near the surface at times.

The next most northern location was the US Army Corps of Engineers, Lamb's Creek Recreational Area located 3 km (1.9 mi) northwest of Mansfield, Pennsylvania. Plots were located in the flood-plain of the Tioga River, which also forms the storm-water retention basin for Tioga Reservoir. Soil is an Orrville silt loam (Fine-loamy, mixed, active, nonacid, mesic Fluventic Endoaquept) with a high water table and is subject to severe, long-duration flooding when storm water backs up behind the dam. The soil at this site displayed a classic floodplain soil profile. The surface is a very silty silt loam that sits on top of a sandy loam material at around 64 to 76 cm (25 to 30 in). The underlying sand layer was saturated, and based on topographical features, the water appeared to be connected to the stream located about 20 m (66 ft) from the plots. Summertime lake elevation is typically 1.5 m (59 in), and wintertime lake elevation is 0.75 m (30 in) lower than the location of the plots. There was no discernible elevation change within the study area.

The next location to the south was the 11 ha (27 ac) Mattern Watershed located in the Ridge and Valley Physiographic Province of east-central Pennsylvania. The Mattern watershed is situated about 80 km (50 mi) north of Harrisburg, Pennsylvania, within the larger 726 ha (1,794 ac) Mahantango Creek watershed, a tributary of the Susquahanna River. Plots were located near the channel of an ephemeral first order stream at the headwaters of the watershed. Plots were sown perpendicular to the stream, with an elevation difference of approximately 20 cm (8 in) from the top to bottom of the plots. The upstream half of the plots is mapped as Berks, a well drained, moderately deep soil classified as a loamy-skeletal, mixed, active, mesic Typic Dystrudept. The downstream soils belonged to the Albrights series, which is an associated moderately well to somewhat poorly drained soil with a fragipan at 45 to 60 cm (18 to 24 in) depth that formed in similar parent materials. The Albrights series is classified as a fine-loamy, mixed, semiactive, mesic Aquic Fragiudalf. The site experiences prolonged surface saturation during winter and periods of extensive precipitation, but the water table can descend to below 2.5 m (8.2 ft) during summer drought. Distinct grey and reddish brown redox features were observed in the Albrights but not the Berks soils. The channel did not consistently contain flowing water. The majority of water in the channel originates from subsurface base flow, supplemented by periodic runoff following rainstorms. No long-term surface flooding occurs.

The southernmost site was located at the University of Maryland, Wye Research Center on the Maryland eastern shore. Plots were located near sea level on the Mid-Atlantic Coastal Plain about 350 m (1,150 ft) from an inlet of the Chesapeake Bay. The site paralleled but was not immediately adjacent to a stream. The plots sloped toward the stream with an elevation difference of approximately 30 cm (12 in). The soils are mapped as Mattapex, a moderately well-drained soil formed in silty eolian sediments that are underlain by coarser fluvial or marine sediments. The Mattapex is classified as a fine-silty, mixed, active, mesic Aquic Hapludult. Other soils at the site included the Othello series, an associated poorly drained soil formed in similar parent materials classified as a fine-silty, mixed, active, mesic Typic Endoaquult, and the Zekiah series, a poorly drained soil formed in loamy alluvium classified as a coarse-loamy, siliceous, active, acid, mesic Typic Fluvaquent. The upslope portion of the plots matched the Mattapex series, whereas the downslope portion matched the Zekiah and Othello series. Indications of soil saturation, including distinct grey and reddish redox features, were observed in both surface and subsurface horizons throughout the site.

Approximately 13 months after transplanting (May 17, 2005, at Wye and June 14 to 22, 2005, at the northern sites) survival was determined for each plant; then crown width and vegetative plant height were measured for all surviving plants. Crown width was measured as the diameter of the crown in the within-row direction. Plant height was measured as the height of the majority of tillers on each plant. Because vegetative plant height and crown width were highly correlated, only crown width data will be presented. Sites were harvested from north to south, beginning on November 2, 2005, at Big Flats and finishing on November 9, 2005, at Wye. Aboveground biomass was harvested at a cutting height of 15 cm (6 in). Plants were harvested in groups of five plants, representing the bottom, middle, and top positions when moving away from the stream bank. Harvested materials were oven dried at 55°C (131°F) for 48 hours and were weighted to determine biomass. Data collection procedures in 2006 were similar to 2005. Survival, crown width, and vegetative height were determined on May 9, 2006, at Wye, and between June 7 and 12, 2006, at the three northern locations. Aboveground biomass harvests occurred between October 31 and November 7, 2006, at the northern locations, and on November 21, 2006, at Wye.

Data were analyzed using the SAS Proc GLM procedure (SAS 2002) as a randomized block design with locations and cultivars treated as fixed effects. Cultivars were replicated four times at each location. Plots were laid out such that replications paralleled the stream bank or other water course, and the three rows of each treatment were oriented perpendicular to the stream. At Big Flats, two replications were placed on one side of the stream and two were placed on the opposite bank. At the other locations, all replications were lined up in a row along the water course. Differences among treatments were declared significant at $p = 0.05$.

Results and Discussion

Greenhouse Screening. In the well-drained pots, gravimetric soil moisture content at the time of harvest was near field-capacity at the bottom of the pot (0.12 g g^{-1}) but was relatively dry at the top (0.05 g g^{-1}), despite daily irrigation applications. Rapid water extraction and drying of the surface soil resulted from extensive root development in the upper soil layer. Soil moisture content in the waterlogged pots was 0.16 g g^{-1} in the middle and 0.18 g g^{-1} near the bottom of the pots. The top layer was also wetter than in the well-drained pots (0.08 g g^{-1}).

Table 2

Root tolerance to saturated soil condition (ratio of root length in middle section of saturated treatment to root length in middle section of control treatment) and aerenchyma content of root collected from just below the boundary layer between the saturated and well-watered but unsaturated zones. Species include switchgrass (SG), prairie cordgrass (PC), Indiangrass (IG), eastern gamagrass (EG), big bluestem (BB), and little bluestem (LB). Flood tolerance data were square root transformed for analysis then back transformed for presentation. All data are presented as the mean ± 1 SE. Cultivars named in bold were included in field trial.

Cultivars	Flooding tolerance (Saturated/control)	Saturated aerenchyma (%)	Control aerenchyma (%)
Red River PC	**1.32 ± 0.12**	**93 ± 3**	**98 ± 1**
Shelter SG	**1.21± 2.72**	**73 ± 0**	**86 ± 3**
Osage IG	**0.96 ± 0.62**	**67 ± 30**	**96 ± 1**
Hightide SG	**0.81± 1.54**	**80***	**56 ± 14**
Cave-N-Rock SG	0.69 ± 0.52	89 ± 6	83 ± 2
Pete EG	0.62 ± 0.07	91 ± 4	94 ± 1
Blackwell SG	0.38 ± 0.61	96 ± 3	96 ± 2
Rumsey IG	0.19 ± 0.44	86 ± 11	92 ± 6
OH 370 BB	0.18 ± 0.31	52 ± 25	93 ± 4
Tomahawk IG	0.17 ± 0.36	5*	97 ± 1
Forestburg SG	0.17 ± 0.26	93 ± 5	91 ± 4
Meadowcrest EG	**0.16 ± 0.23**	**62 ± 30**	**88 ± 4**
Cheyenne IG	0.13 ± 0.18	96*	98*
Alamo SG	0.10 ± 0.10	44 ± 24	97 ± 1
Kanlow SG	0.08 ± 0.20	86 ± 1	69 ± 23
Dacotah SG	0.07 ± 0.25	99*	96 ± 1
Contract SG	0.05 ± 0.06	62 ± 24	82 ± 11
Kaw BB	0.05 ± 0.05	nd†	54*
Suther BB	**0.03 ± 0.10**	**49 ± 47**	**64 ± 14**
Round Tree BB	0.03 ± 0.10	88*	94 ± 4
Suther IG	**0.03 ± 0.06**	**nd**	**97 ± 2**
Earl BB	0.02 ± 0.11	86 ± 4	97 ± 1
Niagara BB	**0.01 ± 0.05**	**29 ± 26**	**98 ± 1**
Suther LB	0.00 ± 0.00	nd	75*
Bonilla BB	**0.00 ± 0.00**	**nd**	**96 ± 2**
Bison BB	0.00 ± 0.00	nd	96*

* Only one sample per cultivar was available for aerenchyma determination.

† Aerenchyma content not determined because of insufficient root material.

Roots from all 26 cultivars reached the bottom of the 120 cm (48 in) deep pots after three months growth under well-drained conditions (data not shown). In contrast, only Red River PC extended its roots to the bottom of the pot when the lower half of the soil was waterlogged. Two cultivars, Red River PC and Shelter SG had greater root length in the saturated compared with the control soils (table 2). Among the species where several cultivars were tested, the big bluestems had generally poor root growth into saturated soil, whereas switchgrass and Indiangrass cultivars exhibited a wide range of tolerances. It was clear that the ability of a cultivar to extend roots into waterlogged soils had to be evaluated under waterlogged conditions and could not be inferred from optimal soil moisture conditions.

Twenty-one of the 26 cultivars could be evaluated for aerenchyma formation in saturated soils (table 2). Three cultivars, Suther LB and Bonilla and Bison BB had no roots that extended into the saturated soil, and Suther IG and Kaw BB had so few roots that we were unable to collect large enough samples for aerenchyma determination. All cultivars evaluated were aerenchymous to some extent, although a great amount of variability existed for aerenchyma development, even within cultivars and water treatments. All cultivars exhibited extensive aerenchyma formation when the pots were allowed to drain freely. Although a valid statistical test could not be conducted due to lack of randomization between saturated and drained pots, the well-drained treatment appeared to have greater aerenchyma content than the saturated treatment (89% versus 71%, respectively). Within-treatment variability was great enough that few significant differences in aerenchyma formation could be observed for the cultivar by saturation level interaction. However, five cultivars, Alamo and Shelter SG, Niagara, and OH370 BB, and Tomahawk IG, exhibited significant reductions in aerenchyma content under saturated conditions. No cultivar showed a significant increase in aerenchyma formation when soils were saturated, although Hightide

SG exhibited a trend toward higher aerenchyma content.

Root morphological features characteristic of species adapted to saturated soils commonly include a strong barrier to radial oxygen loss and extensive aerenchyma formation under both saturated and nonsaturated conditions (McDonald et al. 2002). The presence of aerenchyma creates internal diffusive pathways, which increase root porosity and facilitate internal oxygen diffusion (Visser et al. 2000b) and has been closely connected with the growth rate of new roots (Laan et al. 1989). Justin and Armstrong (1987) examined 91 plant species from wetland, intermediate, and nonwetland habitats, and found that depth of root penetration into flooded soil increased with increasing root porosity.

In the greenhouse study, extensive aerenchyma formation was found in the best performing cultivars but was not necessarily associated with improved root growth under waterlogged conditions. There was no significant relationship between aerenchyma formation and root growth under saturated conditions ($r^2 = 0.07$, $p = 0.53$). However, all cultivars with <50% aerenchyma content under saturated conditions performed poorly and had little root growth into the waterlogged soil. At the same time, Cheyenne IG, Kanlow SG, Dacotah SG, Roundtree BB, and Earl BB all had >85% aerenchyma, yet still had poor root growth into the saturated zone.

Miller-Goodman et al. (1997) found that aerenchyma were present in switchgrass, big bluestem, Indiangrass, and eastern gamagrass cultivars growing in well-aerated conditions, but in the little bluestem cultivar they examined (cv. Aldous), aerenchyma only developed with exposure to hypoxia. No cultivar in the greenhouse study showed a significant increase in aerenchyma formation when soils were saturated, contrary to other reports that flooding enhances aerenchyma formation (Vasellati et al. 2001; Jiang and Wang 2006). However, others have observed aerenchyma production to be as high in drained as in flooded conditions (Jackson et al. 1985).

Reduced aerenchyma formation in the saturated treatment could have been an indirect result of the reduced root growth into the saturated zone. All root segments were collected at a uniform distance from the top of the pot rather than at a set distance from the root apex. Because of their reduced growth, root segments sampled in the saturated treatment could have been closer to the root tip than those sampled in the control treatment. The root cortex typically remains nonaerenchymous throughout the extension zone with cell destruction beginning several millimeters behind the axis (Justin and Armstrong 1987). As such, root porosity can be low near the apex but then increase as distance from the apex increases (Laan et al. 1989). It is possible that younger tissues, with less fully developed aerenchyma, were sampled in the saturated treatment.

As a group, the big bluestem cultivars tended to have relatively low aerenchyma content and poor growth into poorly aerated soils. In this study, switchgrass and Indiangrass results were the most variable. Alamo and Contract SG had poor aerenchyma development and little root growth, Dacotah had extensive aerenchyma development but poor root growth, and Shelter had moderate aerenchyma development but the greatest flood tolerance ratio of any cultivar used in the study. Other switchgrass cultivars were intermediate in root growth and aerenchyma development. Osage IG also had only moderate aerenchyma development but ranked third in flooding tolerance, whereas Suther IG had so little growth into the saturated zone that it was not possible to make aerenchyma measurements.

Red River PC was the only cultivar to extend its roots to the bottom of the saturated pots. Prairie cordgrass is typically found on wet prairie sites and has been studied for inclusion in prairie and urban wetland restorations (Bonilla-Warford and Zedler 2002; Fraser and Kindscher 2005). The relatively slow root growth of Red River prairie cordgrass in the well-drained pots supported the observation by McDonald et al. (2002) that anatomical features that facilitate growth in waterlogged soils may cause limitations for root function under well-drained conditions. Unfortunately, this was the only prairie cordgrass cultivar that we evaluated, but the performance of Red River suggests that this species deserves further evaluation. Suitable plant materials for inclusion in riparian buffers were found among many warm-season species. The six best performing cultivars in terms of relative root growth into saturated soil were from four different species. Some species, however, such as prairie cordgrass, appear to be more likely than others, such as big bluestem, to provide cultivars that are tolerant of anaerobic soils.

Field Study. Plots at Big Flats were located along the bank of a small stream that was subject to periodic flooding. Some of the wettest periods occurred during the establishment year of 2004. From September 8 to 11 and from September 17 to 20, portions of the plots were underwater for a total of 130 hours. Stream depth was high enough during both occasions to briefly flood even the highest plants on the stream bank. Plots were also partially flooded on three occasions in 2005 and five times in 2006. Mean duration of all flooding events from 2004 to 2006 was 31 hours, with a range of 2 to 100 hours. Mean depth to the water table throughout the experiment was 80 cm (31 in) near the stream and 83 cm (33 in) at the top of the bank.

The Lamb's Creek site experienced significant flooding, especially in the autumn of 2004 and early spring of 2005. Lamb's Creek received 585 mm (23 in) rainfall during July through September 2004, culminating with passage of remnants from hurricane Ivan in September. Plots were submerged beneath lake waters for 2 days from September 10 to 11 and again for 7 days from September 18 to 24 following the passage of Ivan. Lake depth at the plot site was 8.24 m (27 ft) on September 19. Plots were again covered with water from January 14 to 17, March 29 to 31, and April 3 to 9, 2005. When examined in May 2005, all plants remained in place where they had been transplanted but were covered with a 5 to 10 mm (0.2 to 0.4 in) layer of silt. Other minor flooding occurred during winter 2005/2006 and summer 2006. In total, plots were flooded eight times for an average duration of 4.25 days and to an average depth of 3.8 m (12.5 ft).

Water table data are missing from the Mattern site with the exception of April 27 to December 20, 2005. Precipitation was below normal in 2005 (938 mm [36.9 in]), and average depth to the water table during the 2005 growing season (May to September) was 1.87 m (6.1 ft). The Mattern watershed also experienced the effects of Hurricane Ivan, receiving 198 mm (7.8 in) rainfall in September 2004. One other period of heavy rainfall affected the plots in 2006, when 148 mm (5.8 in) was received during a four-day period from June 25 to 28. Average depth to the water table during December 2005 was 25 cm (10 in), suggesting along with visual observations, that the water table was close to the surface during the nongrowing season. Overall precipitation during

2006 was near normal at 1,088 mm (42.8 in), while 2004 was slightly above normal at 1,145 mm (45.1 in).

Rainfall was slightly below normal at the Wye Research Center during the establishment year in 2004 (1,036 mm [40.8 in]) but increased to slightly above normal in 2005 (1,154 mm [45.4 in]) and 2006 (1,188 mm [46.8 in]). During winter months (November to March) depth to the water table averaged 20 cm (8 in), with a range of 0 to 60 cm (0 to 24 in). Average depth to the water table was about 40 to 100 cm (16 to 39 in) during the growing season.

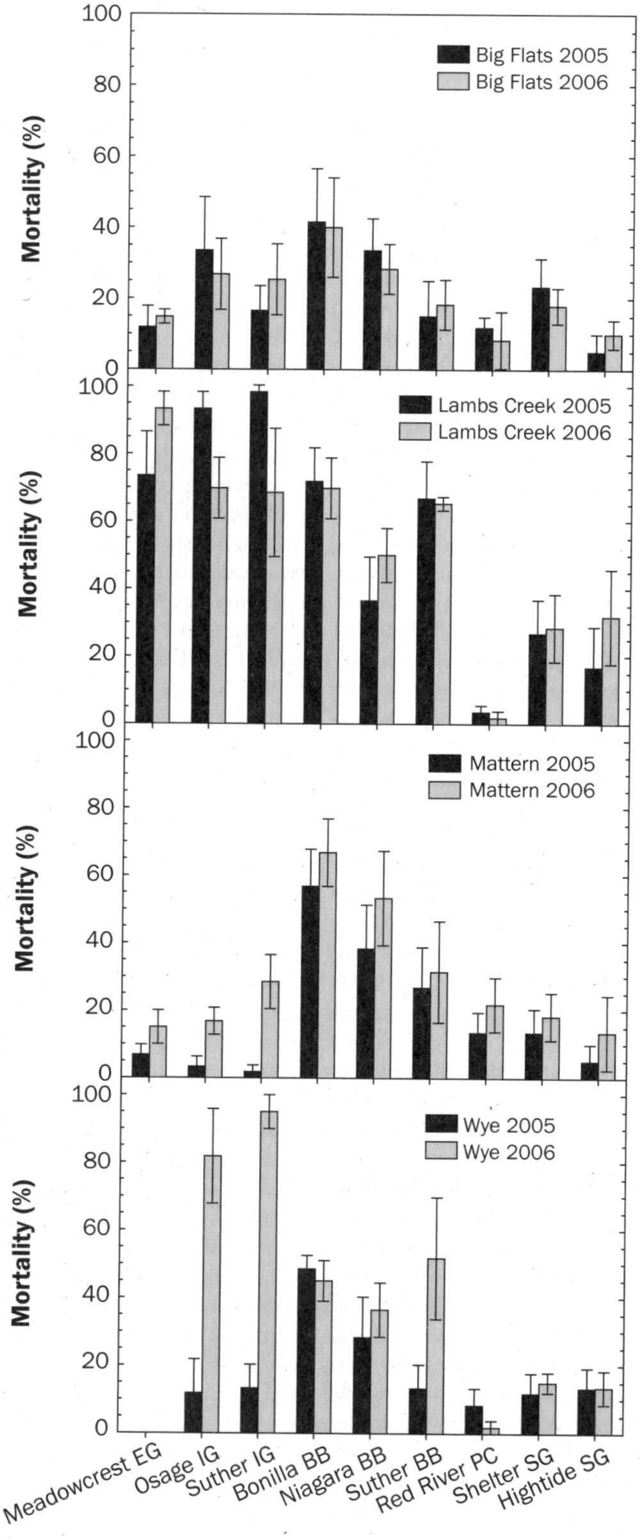
Averaged across cultivars and locations, 35% of the plants transplanted in the spring of 2004 had died by early summer 2006. Mortality was greatest at Lamb's Creek (53%) and was lowest at Big Flats (21%). Most of the plants that died did so in the first year following transplanting, resulting in 28% mortality by early summer 2005 when averaged across locations and cultivars. The Mattern and Wye sites showed increased mortality in 2006 compared with 2005 ($p < 0.01$), whereas there was no difference in mortality between years for Big Flats or Lamb's Creek.

Mortality rates for individual cultivars were significantly affected by both year and location ($p < 0.01$) (figure 1). Mortality rates were low at all locations for Red River PC, Shelter SG, and Hightide SG. Meadowcrest EG also had low mortality at all sites except for Lamb's Creek, where 93% of the plants had died by the end of the experiment. Big bluestem cultivars generally had poor survival with the exception of Suther BB at Big Flats, which had mortality rates at that site that were similar to the best performing cultivars. Indiangrass cultivars showed excellent survival at Mattern and Wye in 2005, but Indiangrass mortality increased significantly at those two sites in 2006. Suther BB also had increased mortality in 2006 compared with 2005. These were the only locations and cultivars where mortality significantly increased from 2005 to 2006. Indiangrass mortality appeared to decrease at Lamb's Creek in 2006 compared with 2005. Surviving plants were very small in 2005, and it is possible that some survivors were buried under the silt deposited by the flooding in autumn 2004 and, thus, were not visible when mortality counts were made in 2005.

Crown width, averaged across locations and cultivars, increased from 10.7 cm (4.2

Figure 1

Plant mortality rates measured in early summer for nine warm-season grass cultivars transplanted into riparian zones at four locations in Big Flats (New York), Lambs Creek (Pennsylvania), Mattern (Pennsylvania) and Wye (Maryland). Species include switchgrass (SG), prairie cordgrass (PC), Indiangrass (IG), eastern gamagrass (EG), and big bluestem (BB). Error bars represent ± 1 standard error.



in) in 2005 to 14.8 cm (5.8 in) in 2006 ($p < 0.01$). Averaged across locations, crown width also increased for all cultivars with the exception of Suther IG, which remained unchanged at about 10 cm (3.9 in) in both years. By 2006, crown width was greatest at Wye (17.4 cm [6.9 in]), followed by Mattern (14.1 cm [5.6 in]) and Big Flats (13.9 cm [5.5 in]), which did not differ from each other, with Lamb's Creek (12.6 cm [5.0 in]) having the smallest crowns. As with plant mortality, year × location × cultivar interaction existed for crown width ($p < 0.01$) (figure 2). Red River PC and Meadowcrest EG had the greatest crown width at all locations, except for Lamb's Creek, where Red River PC did not perform better than the other cultivars.

A significant year × location interaction existed for harvested biomass in the fall. The Wye location had the greatest biomass in 2005, followed by Big Flats, Mattern, and Lamb's Creek (figure 3). Average biomass increased at all locations in 2006, except for Wye, which experienced a significant reduction in plant biomass. The reduction at Wye occurred for all cultivars except for Hightide SG and Meadowcrest EG. Big Flats had the greatest biomass in 2006, followed by Wye, Mattern, and Lamb's Creek. Averaged across locations, Hightide SG and Meadowcrest EG had the greatest biomass, whereas the big bluestem and Indiangrass cultivars had the least. Because of its rhizomatous growth, Red River PC had relatively thin, widely dispersed stems so that its biomass production was relatively low compared with its high survival and vigor. Prairie cordgrass biomass was greatest at Lamb's Creek, where all other cultivars performed relatively poorly.

In the field study, site conditions differed greatly between the northern and southern locations. Both the Mattern and Wye sites experienced fluctuating water tables that periodically reached the soil surface, but neither site experienced surface flooding. Conversely, the Big Flats and Lamb's Creek sites experienced several episodes of surface flooding. Casanova and Brock (2000) found that the depth, duration, and frequency of inundation events affected plant survival and community composition, with duration of flooding having the greatest effect. Some species are apparently highly vulnerable to partial submergence, whereas soil saturation alone has no negative consequence for survival (Visser et al. 2000a). In the current study, the most severe flooding occurred at

Figure 2

Crown width measured in early summer of 2005 and 2006 for nine warm-season grass cultivars transplanted into riparian zones at four locations in Big Flats (New York), Lambs Creek (Pennsylvania), Mattern (Pennsylvania) and Wye (Maryland). Species include switchgrass (SG), prairie cordgrass (PC), Indiangrass (IG), eastern gamagrass (EG), and big bluestem (BB). Error bars represent ± 1 standard error.

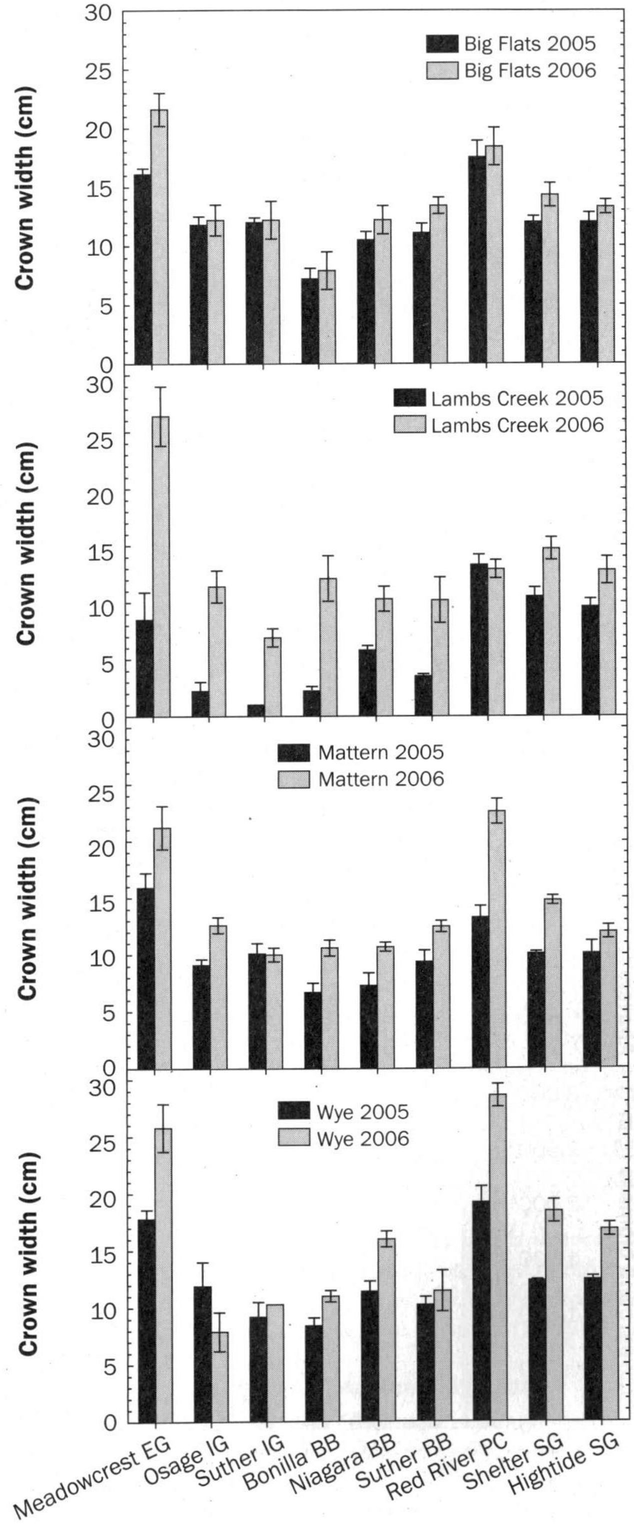
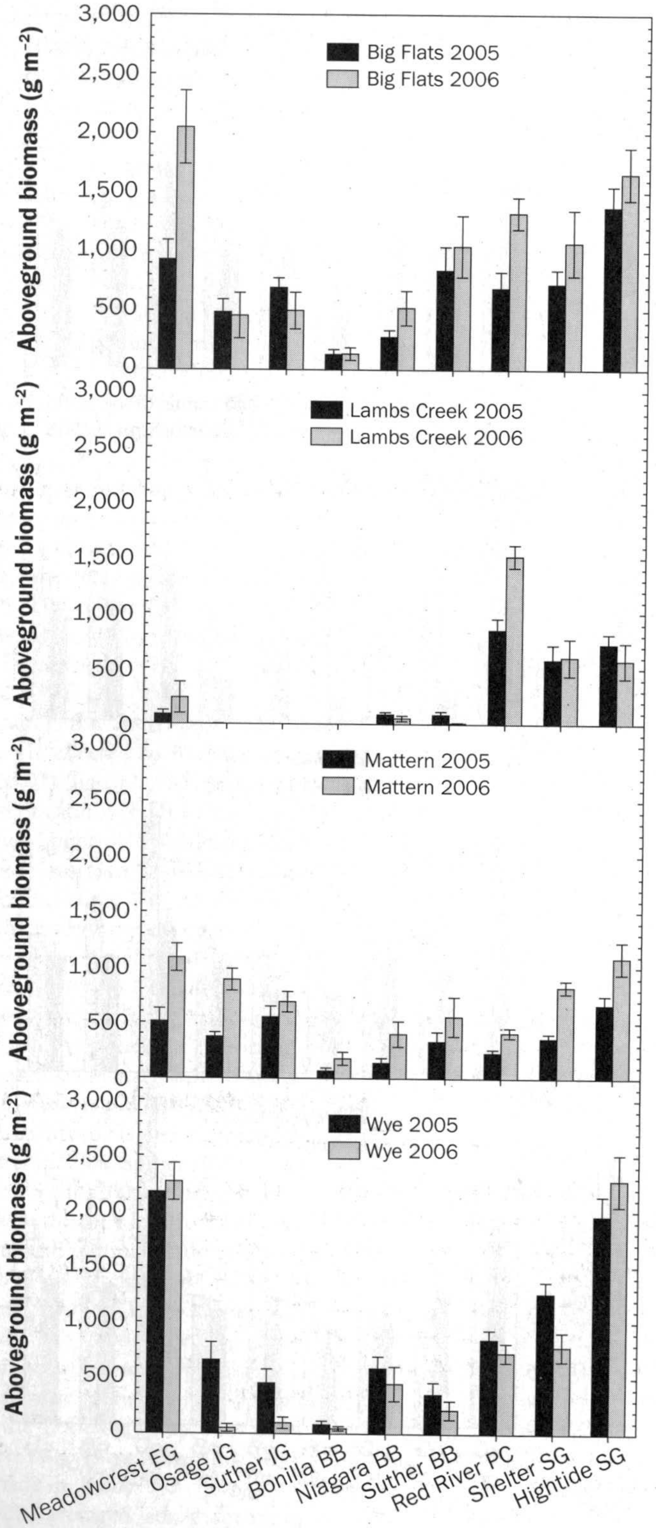


Figure 3

Aboveground biomass measured in the autumn of 2005 and 2006 for nine warm-season grass cultivars transplanted into riparian zones at four locations in Big Flats (New York), Lambs Creek (Pennsylvania), Mattern (Pennsylvania) and Wye (Maryland). Species include switchgrass (SG), prairie cordgrass (PC), Indiangrass (IG), eastern gamagrass (EG), and big bluestem (BB). Error bars represent ± 1 standard error.



Lamb's Creek, where the plants were completely submerged for several days at a time on several occasions. Plots at Big Flats were also flooded on several occasions. However, plants near the stream at Big Flats were never completely covered for more than a few hours, and only the bases of plants near the top of the stream bank were ever submerged. Plant mortality at Big Flats and Lamb's Creek did not change from 2005 to 2006, indicating that all plants that died did so as a result of flooding during the establishment year of 2004. Subsequent flooding in later years caused no further mortality. In an experiment involving young plants, Klimesova (1994) found that plants flooded in autumn had better survival and growth than those flooded in spring or summer. Presumably, the increased size in the autumn improved chances for survival. Alternatively, the plants may have been dormant in the fall and less susceptible than actively growing plants.

With a few exceptions noted below, cultivar performance was consistent across sites. Red River PC, Meadowcrest EG, and Hightide and Shelter SG consistently ranked as the top four cultivars for survival, vigor, and biomass production; Suther BB and Osage IG were intermediate; while Niagara BB, Suther IG, and Bonilla BB were consistently the lowest ranking cultivars (table 3). For the most part, cultivar responses in the field could be predicted by performance in the greenhouse screening study. Notable exceptions were Osage IG, which was expected to be one of the best cultivars but performed relatively poorly under field conditions and Meadowcrest EG, which showed only moderate flooding tolerance in the pot study but was one of the best cultivars at most field locations. The poor performance of Osage IG and the better-than-expected performance of Meadowcrest EG underline the importance of conducting follow-up field trials to confirm results from controlled environment screenings. None of the poorest performing cultivars in the greenhouse screening subsequently performed well in the field, suggesting that the greenhouse screening could be used as a preliminary effort to eliminate poor-performing germplasm, reserving more expensive and time-consuming field trials for the most promising materials.

Submergence of the plots at Lambs Creek had the most significant impact on Meadowcrest EG. That cultivar had excellent survival at the other three sites but was almost completely eliminated at Lambs Creek. However, the few plants that did survive were relatively large so that Meadowcrest EG had the largest crown width and fourth highest biomass at Lambs Creek. The cultivars with the greatest increase in crown width at Lamb's Creek in 2006 were also the cultivars with the greatest mortality rates, i.e., big bluestem, Indiangrass, and eastern gamagrass. Presumably, increased mortality reduced plant competition, allowing for greater expansion of the remaining plants. The switchgrass and prairie cordgrass cultivars, which had relatively high survival, had little or no increase in crown width. Apparently, Meadowcrest EG could survive and thrive under periodic flooding and high water tables but could not withstand long-term complete submergence.

Niagara BB had relatively good survival and biomass production at Lambs Creek and at Wye compared to its performance at Big Flats and Mattern. Osage and Suther IG had relatively poor survival and growth at all sites except for Mattern, where Osage and Suther ranked third and fourth, respectively, for aboveground biomass and were not significantly different from the two best performing cultivars, Hightide SG and Meadowcrest EG. Red River PC, on the other hand, had much poorer survival and growth at Mattern compared with other sites. The Mattern watershed provided the least stressful environment in terms of flooding stress, yet had the lowest overall plant vigor and aboveground biomass except for Lambs Creek. It is possible that the fragipan underlying the Albrights soil restricted rooting depth, and that drought stress during the summer provided as great or greater constraint to plant growth than did flooding stress during the winter and spring. These conditions were detrimental to Red River PC, which has exhibited drought sensitivity in other studies (Bonilla-Warford and Zedler 2002), while tending to favor the Indiangrass cultivars compared with their performance at the more flood-prone locations.

Table 3

Cultivar rankings for plant mortality, vigor, and aboveground biomass at Big Flats (BF), New York, Lambs Creek (LC), Pennsylvania, Mattern (M), Pennsylvania, and Wye (W), Maryland. Species and cultivars tested included Hightide and Shelter switchgrass; Red River prairie cordgrass; Meadowcrest eastern gamagrass; Suther, Niagara, and Bonilla big bluestem (BB); and Osage and Suther Indiangrass (IG). Cultivars are listed in order of ranking when averaged across the four locations. Mortality rankings were from lowest to highest, with 1 indicating the lowest and 9 indicating the highest mortality. Width and biomass rankings were from highest to lowest, with 1 indicating the greatest width or biomass and 9 indicating the least.

	Location				
Cultivars	BF	LC	M	W	Mean
	Mortality				
Hightide	1	2	1	3.5	1.9
Red River	2	1	6	2	2.8
Meadowcrest	3	8.5	3	1	3.9
Shelter	5	3	5	3.5	4.1
Suther BB	4	5	7	6	5.5
Osage	7	7	2	7.5	5.9
Niagara	8	4	8	5	6.3
Suther IG	6	8.5	4	9	6.9
Bonilla	9	6	9	7.5	7.9
	Crown width				
Meadowcrest	1	1	1	2	1.3
Red River	2	2	2	1	1.8
Shelter	3	3	3	3	3.0
Hightide	4	4	4	4	4.0
Suther BB	5	7	5	6	5.8
Osage	7	5	6	7	6.3
Niagara	8	6	8	5	6.8
Suther IG	6	9	7	9	7.8
Bonilla	9	8	9	8	8.5
	Biomass				
Hightide	1	2	1	2	1.5
Meadowcrest	2	4	2	1	2.3
Red River	3	1	7	4	3.8
Shelter	5	3	5	3	4.0
Osage	7	7	3	6	5.8
Suther BB	4	6	6	8	6.0
Suther IG	6	8.5	4	7	6.4
Niagara	8	5	8	5	6.5
Bonilla	9	8.5	9	9	8.9

Summary and Conclusions

A greenhouse study revealed that root systems of all warm-season grasses tested were aerenchymous under both flooded and non-flooded conditions. Despite the universal presence of aerenchyma, there was a wide range of flooding tolerance, as measured by root growth. This ranged from cultivars with no root penetration into the saturated soil to two cultivars with greater root growth in flooded compared with control treatments. No significant relationship existed between percent aerenchyma and flooding tolerance. Flooding tolerance as determined in the greenhouse study did a reasonably good job of predicting survival and growth under riparian conditions in the field. However, enough differences existed between field and greenhouse results to recommend the need to verify controlled environment results with field studies before recommending cultivars for use in riparian zones.

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